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DIETS OF ABUNDANT FISHES FROM BEACH SEINE CATCHES IN SEAGRASS BEDS OF A TROPICAL BAY (GAZI BAY, KENYA)

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Abstract. The composition of the diet of 14 fish species that were common in beach seine catches over the seagrass beds of Gazi Bay (Kenya) was investigated. Three trophic guilds could be distinguished based on dietary diversity and on the numerical and gravimetrical composition of the diet. *Herklotsichthys quadrimaculatus*, *Stolephorus indicus* and *Atherinomorus duodecimalis* were planktivores. Their stomach fulness index was low and the diet was not diverse. The main food items were harpacticoid and calanoid copepods and brachyuran zoea and megalopae. *Apogon thermalis*, *Fowleria aurita*, *Paramonacanthus barnardi*, *Mulloides flavolineatus*, *Lutjanus fulviflamma*, *L. argentimaculatus* and *Gerres acinaces* were benthivores, mainly feeding on small epi- and hyper-benthic prey. Their diet was very diverse and it was dominated by Amphipoda (Gammaridea), Tanaidacea and Mysidacea. Their fulness indices were low, but a little bit higher than those observed for the planktivores. A third group were the « piscivores » : *Bothus myriaster*, *Fistularia commersonii*, *Sphyraena barracuda* and *Plotosus lineatus*. The dominant items in the food spectrum of these species were postlarval fishes and large nektonic invertebrates (gammaridean amphipods, mysids, shrimp and crabs). Their diet was not diverse and the fulness index was much higher than that of the other species examined. All other species caught were further classified according to the following feeding guilds : herbivores, planktivores, benthivores (epi- and hyperbenthivores) and piscivores. The ichthyofauna of Gazi Bay was clearly dominated by benthivores.

Key words: feeding ecology, trophic organization, fish, seagrass beds, Kenya

INTRODUCTION

This study presents data on the trophic organisation of the fish fauna of a shallow East-African bay (Gazi Bay, Kenya). The fish fauna of Gazi Bay has received considerable attention in recent years (VAN DER VELDE *et al.*, 1994, DE TROCH *et al.*, 1996, KIMANI *et al.*, 1996, WAKWABI & MEES, unpublished data). For this study, fish were sampled in 9 stations with a beach seine over seagrass beds and unvegetated areas. A total of 3601 fishes belonging to 75 species and 40 families were caught (> 95% juveniles). Multivariate analysis of the catch data revealed that 3 communities could be distinguished (DE TROCH *et al.*, 1996) : a first community occurred in the downstream part of the river-fed western creek, were sandy bottoms with sparse seagrass vegetation occur. The fish community was characterised by low density and diversity and is not considered further. The two other communities were characterised by a high fish diversity. One community occurred in the upstream part of the western creek and was dominated by *Gerres acinaces* Bleeker, 1854 and *Atherinomorus duodecimalis* (Valenciennes, 1835). The other community was found in the shallow areas of the bay proper and in the mouth area of the eastern creek. There, the dominant species were *Apogon thermalis* Cuvier, 1829 and *G. acinaces* Bleeker, 1854.

Individuals in the dominant size-classes of the most abundant and characteristic species of these latter communities were selected for analysis of stomach contents. For the remaining fish species caught, information about their trophic guild was taken from the literature and from FISHBASE (1995).

The aim of this study was to investigate the diet of some common fishes whose diet is poorly documented to date and to get an idea of the trophic organisation of fishes in a typical East-African bay.

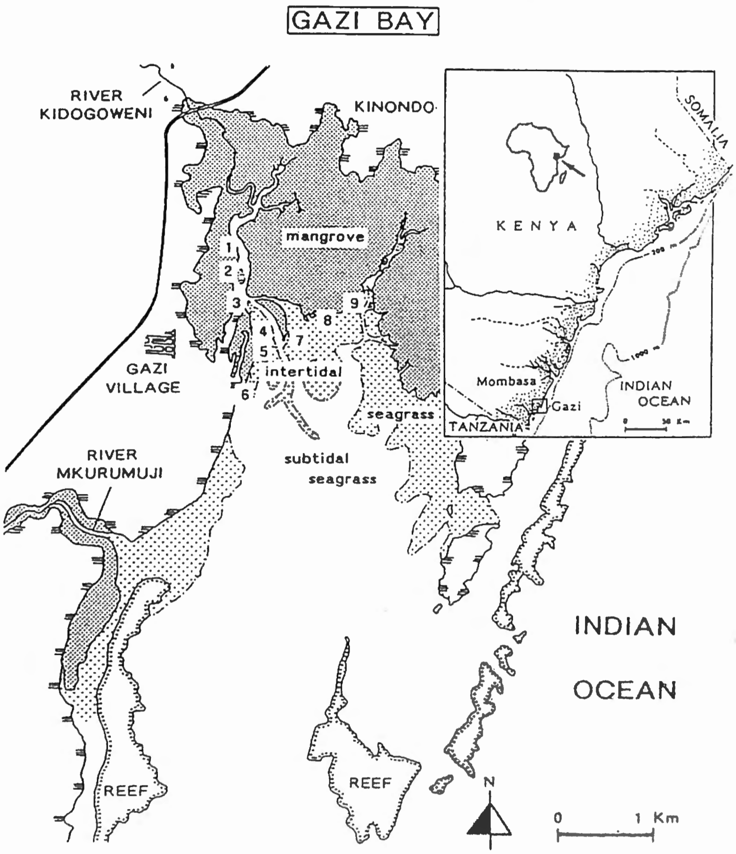

Fig. 1. – Map of Kenya with situation of Gazi Bay (COPPEJANS *et al.*, 1992). Detail of Gazi Bay (SLIM, 1995) with indication of the sampling stations.

MATERIAL AND METHODS

Study area

Gazi Bay (Kenya) is located some 50 km north of the Tanzanian border and 60 km south of Mombasa Island (4°22'S, 39°30'E). The bay is between 1.75 and 3.50 km wide and 3.25 km long and is bordered with mangroves. Two major creeks characterize the system (Fig. 1). The Kidogoweni river enters the bay through the so-called western creek (surface area ± 18 ha). The eastern creek (2.7 ha) has no freshwater input. In both major creeks and in the bay proper dense seagrass beds occur (percentage of cover between 30 and 100% in the creeks and 10 to 30% in the lagoon). The downstream part of the western creek is characterised by a sparse seagrass vegetation on a sandy bottom (SLIM, 1995).

Sampling

Samples were taken from two hours before to two hours after low-water springtide on the 17th (western creek) and 18th of August 1993 (eastern creek) with a beach seine net (1.20 m depth, 25 mm stretched mesh size). As the net was 80 m long, a single semi-circular haul was considered to sweep an area of about 509 m^2. All fish were immediately anaesthetized in a benzocaine solution (ethylamino-4-benzoate in seawater) to prevent regurgitation of the stomach content, and subsequently preserved in a 10% formaldehyde-seawater solution.

The location of the sampling stations is shown in Fig. 1. In each station, one sample was taken. Six stations were located in the western creek. The other three samples were taken in the intertidal and shallow subtidal seagrass beds in the eastern part of the bay (mouth of the eastern creek). The seagrass vegetation in each of these sampling stations is discussed by DE TROCH *et al.* (1996).

Diet analysis

In the laboratory all fishes were identified to species level using the keys provided by SMITH & HEEMSTRA (1986) and BIANCHI (1985). The number of individuals per species was counted and the standard length (SL) was measured to the nearest millimetre.

For all common species (>10 individuals) on which no dietary data was available, the length-frequency distribution was used to select the dominant length class. A list of species examined in this study, together with the length class and the sampling station is given in Table I.

A total of 456 fishes were selected for diet analysis. The fishes were dissected and the entire stomach was removed. For *Atherinomorus duodecimalis* (Valenciennes, 1835), *Mulloides flavolineatus* (Lacepède, 1801), *Fistularia commersonii* Rüppell 1838, *Gerres acinaces* Bleeker, 1854, *Lutjanus fulviflamma* (Forsskål, 1775) and *Lutjanus argentimaculatus* (Forsskål, 1775) the content of the stomach and the digestive tracts was considered as the stomach content *sensu lato.* All items present in the stomachs were identified to a high taxonomic level (Table II) and counted. The average number of prey (and prey biomass) per individual is indicated in the results as an indication for the difference in prey

TABLE II

List of the assigned biomass values, the length-ashfree dry weight (AFDW) and other morphometric regressions used to calculate the biomass of the different prey items. All lengths (L), total lengths (TL) and carapax width (CW) are in mm; all dry weights (DW), ashfree dry weights (AFDW) and assigned values are in mg

Nematoda	assigned value: 0.003
Foraminifera	assigned value: 0.001
Annelida	
Oligochaeta	$\ln \mathrm{AFDW} = -6.030 + 1.813 \ln \mathrm{L}$
Polychaeta	$\ln \mathrm{AFDW} = -7.139 + 2.489 \ln \mathrm{L}$
Mollusca	
Bivalvia	$\ln \mathrm{AFDW} = -4.052 + 2.817 \ln \mathrm{L}$
Crustacea	
Copepoda	
Calanoida	assigned value (adult): 0.016
Harpacticoida	assigned value (copepodite): 0.002
	assigned value (adult): 0.004
Ostracoda	assigned value: 0.014
Cladocera	*Daphnia* species: 0.01
Peracarida	
Cumacea	$\ln \mathrm{AFDW} = -6.078 + 2.525 \ln \mathrm{TL}$
Mysidacea	
Mesopodopsis spec.	$\ln \mathrm{AFDW} = -6.107 + 2.867 \ln \mathrm{SL}$
Other Mysidacea	$\ln \mathrm{AFDW} = -6.120 + 2.994 \ln \mathrm{SL}$
Isopoda (idem *Tardigrada*)	$\ln \mathrm{AFDW} = -5.857 + 2.863 \ln \mathrm{TL}$
Amphipoda	
Gammaridae	$\ln \mathrm{DW} = -6.301 + 2.849 \ln \mathrm{SL}$
Corophidae	$\ln \mathrm{DW} = -6.435 + 2.681 \ln \mathrm{SL}$
Other Amphipoda	$\ln \mathrm{AFDW} = -5.857 + 2.863 \ln \mathrm{TL}$
Tanaidacea	$\ln \mathrm{DW} = -4.241 + 1.644 \ln \mathrm{SL}$
Eucarida - Decapoda	
Caridea	
Crangon crangon	$\ln \mathrm{AFDW} = -7.684 + 3.321 \ln \mathrm{TL}$
	$\mathrm{TL} = -0.6 + 8.7\ \mathrm{AP}$
	$\mathrm{TL} = -0.4 + 3.82\ \mathrm{CL}$
	$\mathrm{TL} = -0.4 + 6.1\ \mathrm{TE}$
Brachyura	
zoea	assigned value: 0.050
megalopa	assigned value: 0.189
adult	$\ln \mathrm{AFDW} = -3.967 + 3.164 \ln \mathrm{CW}$
Pisces	$\ln \mathrm{AFDW} = -7.851 + 3.460 \ln \mathrm{SL}$
fish eggs	assigned value: 0.025

A standardized way to measure or evaluate the weight (DW, dry weight) of the ingested food, is to express the amount of food as a percentage of the total fish weight, according to the formula for the fulness index (FI) defined by HUREAU (1969) (BERG, 1979):

$$FI = \frac{DW\ of\ stomach\ content}{total\ body\ DW} x\ 100$$

To estimate the dry weight of the stomach content, this content was dried during 5 days at 60°C and weighted to 0.1 mg using a Sauter-balance.

The fulness index was not calculated for *Plotosus lineatus* (Thunberg, 1787) and *Sphyraena barracuda* (Walbaum, 1792) as the dry weight of these large species was not estimated. Empty stomachs were not included in the calculations.

To assess niche breadth the Shannon-Wiener diversity index (HILL, 1973) was calculated as:

$$H' = \sum_{i=1}^{n} p_i (\log p_i)$$

$$with\ p_i = \frac{N_i}{N_t} = relative\ abundance\ of\ prey\ item_i$$

RESULTS

Diet composition of dominant species

The stomach contents of the examined species are discussed in terms of numerical (%N) and gravimetrical (%G) percentages (Figs 2-3).

Herklotsichthys quadrimaculatus (Rüppell, 1837) (Blueline herring)

An average of 93 prey items was present in the ingested contents per individual. This average corresponds to a biomass of 3.3 mg AFDW per individual.

Numerically, harpacticoids were the dominant prey (69.7% of the total number of ingested prey). Other important prey items were brachyuran zoea larvae and Mollusca (mainly gastropods), which accounted for 9.3%N and 8.4%N, respectively. Ostracods (4.2%) and calanoid copepods (3.4%) were less important in the total food spectrum. Other prey items were brachyuran megalopa larvae (1.7%), isopods (1.4%N), tanaids (0.9%N) and gammaridean amphipods (0.3%N). Gravimetrically, the diet was dominated by megalopa larvae (54.2%G) and molluscs (17.3%G). The numerically dominant harpacticoids represented only 7.8% of the total amount of ingested biomass.

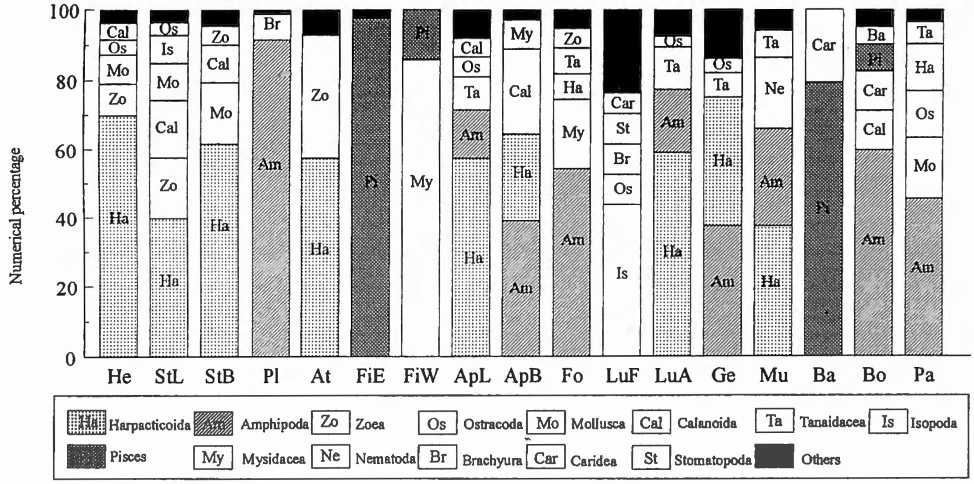

Fig. 2. – Numerical diet composition of the investigated fish species
(abbreviations see Tabel I)

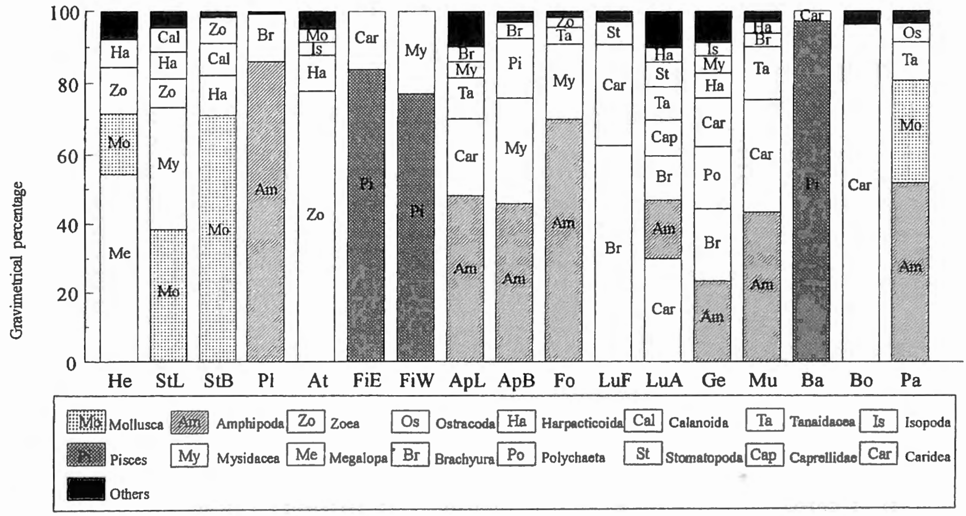

Fig. 3. – Gravimetrical diet composition of the investigated fish species
(abbreviations see Tabel I)

***Stolephorus indicus* (van Hasselt 1823) (Indian anchovy)**

Since the length-frequency distribution of this species was clearly bimodal, individuals of two length classes were considered : 40-45 mm : StS (*Stolephorus indicus* small) and 70-75 mm : StL (*Stolephorus indicus* large).

An average number of 11.2 prey items was found in the individuals of the 40-45 mm length class. This corresponds to an average biomass of 0.6 mg AFDW. Individuals of the second length class contained an average of 38.4 prey and 0.46 mg AFDW per individual.

In both length classes harpacticoids were numerically dominant (39.8%N for StS, 61.7%N for StL). Other important prey were zoea larvae (17.7%N for StS, 5.2%N for StL), calanoids (16.8%N for StS, 10.7%N for StL) and molluscs (mainly gastropods) (10.6%N for StS, 17.7%N for StL). The diet resembles that of *Herklotsichthys quadrimaculatus* in terms of prey species, but not in the relative importance of each item *e.g.* calanoids were more important in the foodspectrum of *S. indicus*.

In terms of biomass, the Indian anchovy mainly utilised molluscs (gastropods) (38.4%G for StS, 71.0%G for StL). The main difference between both length classes was the contribution of mysids to the diet: these were absent from the stomachs of the larger (70-75 mm) individuals, while they formed an important prey (35%G) for the smaller (40-45 mm) individuals.

***Plotosus lineatus* (Thunberg 1787) (Striped eel-catfish)**

An average of 37 prey items was found in the stomachs analysed. This corresponds to an average biomass uptake of 111 mg AFDW per fish. Numerically, the diet was dominated by amphipods (90.7%N) and Brachyura (8.4%N). The remaining prey (0.9%N) were Polychaeta and Caridea. The gravimetrical composition was also dominated by amphipods (85.6%G) and Brachyura (14.1%G). The other prey items counted for only 0.4% of the biomass.

***Atherinomorus duodecimalis* (Valenciennes 1835) (Tropical silverside)**

An average of 170 prey items per individual was found, corresponding to an average biomass of 3.9 mg AFDW per fish. The food spectrum was dominated by harpacticoids (57.5%N) and zoea larvae (35.4%N). Calanoids (2.7%), isopods (1.4%), molluscs (1.3%) and prey species that were only occasionally found (foraminifers, ostracods, megalopa larvae, amphipods, brachyurans, tanaids, oligochaetes and shrimp) together accounted for 7.1%N of the diet.

Zoea larvae (77.6%G) dominated in gravimetrical terms. The tropical silverside contained an average of 3 mg AFDW of zoea larvae per individual. The numerically dominant harpacticoids represented 10.1% of the total gravimetrical composition. The other prey items were quite negligible in the total ingested biomass.

***Fistularia commersonii* (Rüppell 1838) (Smooth flutemouth)**

The diets of individuals of the smooth flutemouth from the eastern creek (FiE) and the western creek (FiW) were compared.

In the analysis of the specimens from the eastern creek (FiE), an average of 4 prey items was found (14.8 mg AFDW). The dominant prey item was Pisces (97.6%N). Caridea and Amphipoda both accounted for 1.3%N. The importance of fish is also shown in the gravimetrical composition, where they constituted 83.7% of the ingested biomass. Caridea were more important gravimetrically (16.3%G) than numerically.

An average of 28 prey items per fish was found (18.1 mg AFDW) in the individuals from the western creek (FiW). Here mysids (86%N), 23.9 mysids per fish, dominated the diet. Pisces represented 14%N. The gravimetrical composition was similar to that of the individuals from the western creek. The major part was formed by fish (76.8%G). This corresponds to an average of 4.2 mg AFDW per individual. The remaining 23.2%G was mysids.

Apogon thermalis (Cuvier 1829) (Masked cardinal)

The individuals of the masked cardinal were taken from the eastern (30-33 mm standard length : ApE) and the western (35-38 mm standard length : ApW) creek.

In the individuals of the eastern creek, an average of 10.5 prey per individual was found (average biomass : 0.7 mg AFDW per fish). The masked cardinal fed primarily on harpacticoids (57.6%N). The other half of the diet consisted of gammaridean amphipods (13.9%N), tanaids (9.5%N), calanoids (5.7%N) and ostracods (5.1%). The 'other' prey (8.2%) were mysids, caridean shrimp, brachyuran crabs, isopods, Caprellidea, tardigrads and molluscs. The gravimetrical composition was dominated by Amphipoda (48.1%G) and Caridea (21.9%G).

The individuals of the western creek contained an average of 9 prey items per individual (0.9 mg AFDW per fish). Compared to the individuals of the eastern creek, the same prey items were consumed but amphipods (39.3%N) were the most important prey. Half of the diet was numerically composed of harpacticoids (25.2%) and mysids (24.4%).

Gravimetrically, the diet was also dominated by amphipods (45.7%G) but mysids (29.9%G) replaced the Caridae from the diet of individuals from the eastern creek . Pisces accounted for 16.6% of the ingested biomass, but were numerically low.

Fowleria aurita (Valenciennes 1831) (Crosseyed cardinal)

An average of 3.7 prey per fish were counted (0.6 mg AFDW per fish). Amphipods were numerically dominant (54.5%N). Mysids accounted for 20% of the total number of ingested prey. Tanaids and harpacticoids both represented 7.3%N, while the numerical percentage of the zoea larvae was 5.5%. The diet was supplemented with calanoids, Caridea and Polychaeta.

The gravimetrical composition emphasizes the importance of amphipods (69.7%G) in the diet. Mysidacea are the second most important source of energy (20.9%G) and tanaids represented 4.7%G.

Lutjanus fulviflamma (Forsskål 1775) (Dory snapper)

Very few prey items (average of 3 per individual) were found per fish, corresponding to an average biomass uptake of 11.9 mg AFDW.

The diet of *L. fulviflamma* (Dory snapper) was numerically dominated by isopods (mainly Sphaeromatidae): 44.1%N. Other important prey were ostracods (8.8%N), brachyurans (8.8%N), stomatopods (8.8%N) and caridean shrimp (5.9%N). The 'other' prey were mainly polychaetes (2.9%N) and unidentified crustacean material (1.1%N).

The gravimetrical composition was principally brachyurans (62.3%G), shrimp (27.3%G) and stomatopods (6.4%G).

***Lutjanus argentimaculatus* (Forsskål 1775) (River snapper)**

An average of 22 prey items per fish was found, corresponding to a biomass of 1.2 mg AFDW.

L. argentimaculatus mainly fed on harpacticoids (59.3%N). A smaller percentage was covered by amphipods (18.1%N), tanaids (12.0%N) and ostracods (3.0%N).

Gravimetrically, the important food sources were shrimp (29.8%G), amphipods (16.8%G), brachyurans (12.7%G), caprellids (10.0%G), tanaids (9.3%G), stomatopods (6.8%G) and harpacticoids (4.2%G).

***Gerres acinaces* (Bleeker 1854) (Smallscale pursemouth)**

The diet of the smallscale pursemouth, with an average of 31 prey items per individual (2.9 mg AFDW), was composed of amphipods (38.0%N), harpacticoids (37.1%N), tanaids (7.4%N) and ostracods (4.5%N). The 'other' prey were isopods, polychaetes and shrimps.

Gravimetrically, the diet is more diverse with prey-items like amphipods (23.6%G), brachyurans (20.8%G), polychaetes (19.2%G), shrimps (13.6%G), tanaids (7.0%G), mysids (4.7%G), isopods (3.8%G), megalopae larvae (2.1%G) and harpacticoids (1.6%G).

The stomach content of *G. acinaces* was characterised by high amounts of detritus (mainly fine macrophytal material) and sediment particles. An average of 85% of the stomach content weight was attributed to sediment and detritus.

***Mulloides flavolineatus* (Lacepède 1801) (Yellowstripe goatfish)**

An average of 20 prey items per fish was found (0.96 mg AFDW). Numerically the diet of the yellowstripe goatfish was dominated by harpacticoids (37.9%N), amphipods (28.3%N) and nematodes (20%N). Other prey were tanaids (7.6%N), ostracods (2.0%N), brachyurans (1.5%N), Caridea (1.0%N), isopods (1.0%N) and polychaetes (0.5%N).

In gravimetrical terms amphipods dominated as they accounted for almost half (43%G) of the ingested biomass. The numerically low Caridea, constituted 31.8% of the gravimetrical composition. Nematodes were gravimetrically insignificant (1.2%G).

***Sphyraena barracuda* (Walbaum 1792) (Great barracuda)**

An average of only 1 prey item per fish was found. Still, the average biomass uptake was 1327.3 mg AFDW per individual. Both numerically and gravimetrically (79.3% N and 97% G), the dominant prey items were Pisces. The diet was supplemented with caridean shrimp (20%N, 3%G).

Bothus myriaster (Temminck & Shlegel 1846) (Disc flounder)

An average of 8 prey items was found per fish (68.5 mg AFDW). Amphipods (60%N) dominated the diet. Calanoids and brachyurans were of secondary importance (both 11%N). Other prey items were Caridea, Pisces, Harpacticoida and Cumacea. Gravimetrically, the diet was dominanted by Caridea (96%G).

Paramonacanthus barnardi (Fraser-Brunner 1941) (Wedgetail filefish)

An average number of 45 prey items and 2.1 mg AFDW was found. Numerically, amphipods dominated the diet (46.1%N). This percentage corresponds to an average of 20 amphipods per fish. The second important prey were gastropod molluscs (almost one fifth). Ostracods and harpacticoids were less important (both 13%N). Other prey were tanaids, isopods, caprellids, foraminifers, tardigrads, calanoids, shrimp, brachyuran zoea larvae and nematodes.

Amphipods (51.5%G) were also dominant in the gravimetrical composition. Molluscs represented one fourth of the gravimetrical composition.

Others

For the remaining species caught the trophic guild to which they belong is given in Table III. This classification is based on information available in the literature and in FishBase (1995).

TABLE III

Species list with number of individuals in the communities of the western (N_{ind} west) and eastern (N_{ind} west) creeks and both communities pooled (N_{total}) together with the trophic guild

species	N_{total}	N_{ind} *west*	N_{ind} *east*	*trophic guild*	*source*
Gerres acinaces	1095	917	178	benthivore	Smith & Heemstra (1986), present study
Atherinomorus duodecimalis	622	622	-	planktivore	present study
Apogon thermalis	228	21	207	benthivore	present study
Herklotsichthys quadrimaculatus	227	225	2	planktivore	Milton *et al.* (1994), present study
Stolephorus indicus	128	128	-	planktivore	Whitehead (1985), present study
Fowleria aurita	100	85	15	benthivore	Sano *et al.* (1984), present study
Plotosus lineatus	88	88	-	piscivore	Van Waeyenberg (1994), present study

species	N_{total}	N_{ind} *west*	N_{ind} *east*	*trophic guild*	*source*
Lutjanus argentimaculatus	87	33	54	benthivore	KULBICKI *et al.* (1993), present study
Leptoscarus vaigiensis	60	2	58	herbivore	SOUSA & DIAS (1981)
Lethrinus lentjan	60	15	45	benthivore	CARPENTER & ALLEN (1989)
Scarus ghobban	55	6	49	herbivore	SANO *et al.* (1984), ANDERSON & HAFIZ (1987)
Lutjanus fulviflamma	53	21	32	benthivore	SANO *et al.* (1984), present study
Scarus spec.	53	42	11	herbivore	SMITH & HEEMSTRA (1986)
Siganus sutor	46	23	23	herbivore	WOODLAND (1990), ROBINS *et al.* (1991)
Fistularia commersonii	46	13	33	piscivore	present study
Leiognathus fasciatus	41	41	-	benthivore	BLABER (1980), FISCHER *et al.* (1990)
Paramonacanthus barnardi	35	7	28	benthivore	present study
Petroscirtes mitratus	28	15	13	herbivore	SANO *et al.* (1984)
Petroscirtes breviceps	28	1	27	herbivore	SANO *et al.* (1984)
Parupeneus barberinus	22	17	5	benthivore	SANO *et al.* (1984)
Sphyraena barracuda	20	18	2	piscivore	RANDALL (1967), present study
Stethojulis strigiventer	19	1	18	benthivore	SANO *et al.* (1984)
Amblygobius albimaculatus	17	3	14	herbivore	SANO *et al.* (1984)
Parascorpaena mossambica	14	9	5	unknown	-
Mulloides flavolineatus	13	2	11	benthivore	present study
Syngnathoides biaculeatus	11	-	11	planktivore	SMITH & HEEMSTRA (1986)
Cheilio inermis	10	-	10	piscivore	SANO *et al.* (1984)
Bothus myriaster	10	10	-	piscivore	present study
Cheilodipterus quinquelineatus	8	-	8	benthivore	SANO *et al.* (1984), PAXTON *et al.* (1989)
Ablennes hians	8	8	-	piscivore	FISCHER *et al.* (1990)
Sebastapistes strongia	7	7	-	unknown	-
Pterois miles	5	1	4	unknown	-
Oplopomus oplopomus	6	-	6	benthivore	SANO *et al.* (1984)
Synodus variegatus	6	5	1	benthivore	PAULIN *et al.* (1989)
Gazza minuta	4	4	-	piscivore	BLABER (1980)
Solenostomus cyanopterus	4	-	4	planktivore	MYERS (1991)
Pelates quadrilineatus	4	-	4	benthivore	SMITH & HEEMSTRA (1986)
Platax teira	3	2	1	unknown	-
Tylosurus crocodilus crocodilus	1	-	1	piscivore	RANDALL (1967), BLABER (1980)
Canthigaster bennetti	3	1	2	herbivore	MYERS (1991)

species	N_{total}	N_{ind} *west*	N_{ind} *east*	*trophic guild*	*source*
Aluterus scriptus	3	-	3	benthivore	Randall (1967), Myers (1991)
Alectis indicus	3	3	-		piscivore Fischer & Bianchi (1984), Fischer *et al.* (1990)
Cheilinus chlorourus	2	2	-	benthivore	Sano *et al.* (1984)
Gerres rappi	2	-	2	benthivore	Woodland (1984)
Upeneus tragula	2	2	-	benthivore	Sano *et al.* (1984)
Ostracion cubicus	2	2	-	herbivore	Myers (1991), Cornic (1987)
Gerres filamentosus	2	2	-	benthivore	Blaber (1980)
Lethrinus harak	2	2	-	benthivore	Carpenter & Allen (1989)
Asterropteryx semipunctatus	2	-	2	herbivore	Sano *et al.* (1984)
Liza macrolepis	2	2	-	herbivore	Skelton (1993), Thomson & Luther (1984)
Dendrochirus brachypterus	2	2	-	unknown	-
Arothron meleagris	2	2	-	herbivore	Randall (1985), Guzman & Lopez (1991)
Trachyrhamphus bicoarctatus	2	2	-	benthivore	Smith & Heemstra (1986)
Leiognathus elongatus	1	1	-	benthivore	James (1984)
Lactoria fornasini	1	1	-	unknown	-
Caranx sexfasciatus	1	1	-	piscivore	Honebring (1990), Salini *et al.* (1994)
Epinephelus spec.	1	-	1	unknown	-
Dactyloptena orientalis	1	1	-	unknown	-
Naso brevirostris	1	1	-	herbivore	Randall (1985)
Parupeneus macronema	1	-	1	benthivore	Fischer *et al.* (1990)
Platax orbicularis	1	1	-	unknown	-
Aulostomus chinensis	1	-	1	piscivore	Randall (1985)
Aeoliscus punctulatus	1	-	1	planktivore	Smith & Heemstra (1986)
Platycephalus indicus	1	-	1	piscivore	Fischer *et al.* (1990)
Chaetodon xanthocephalus	1	-	1	herbivore	Cornic (1987)
Diagramma pictum	1	-	1	benthivore	Jones *et al.* (1992)
Tylerius spinosissimus	1	-	1	unknown	-
Oligolepis acutipennis	1	-	1	benthivore	Sano *et al.* (1984)
Arothron immaculatus	1	1	-	herbivore	Randall (1985)
Neopomacentrus cyanomos	1	1	-	herbivore	Parrish (1989)

Fulness index (FI)

The mean fulness indices together with the standard errors are shown in Fig. 4.

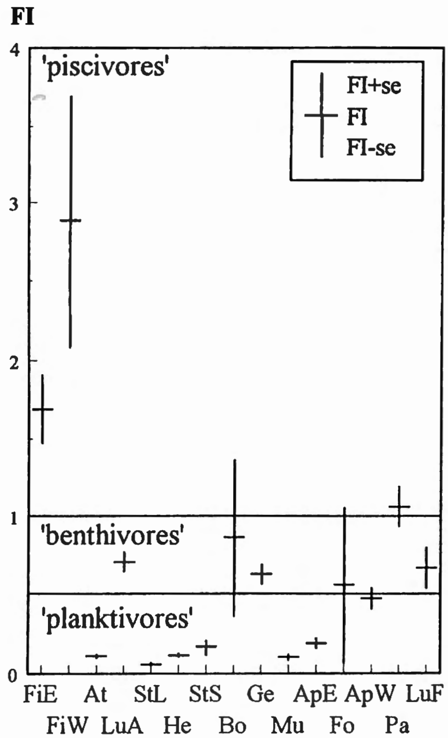

Fig. 4. – Fulness index (FI) together with the standard error (se)

For most species the fulness index was lower than 0.5: *Atherinomorus duodecimalis* (FI = 0.109 ± 0.008), *Stolephorus indicus* (70-75mm) (FI = 0.060 ± 0.011), *Herklotsichthys quadrimaculatus* (FI = 0.115 ± 0.009), *S. indicus* (40-45 mm) (FI = 0.172 ± 0.056), *Mulloides flavolineatus* (FI = 0.102 ± 0.016), *Apogon thermalis* (30-33mm) (FI = 0.189 ± 0.031), *A. thermalis* (35-38mm) (FI = 0.473 ± 0.066).

Five species had a fulness index between 0.5 and 1: *Lutjanus argentimaculatus* (FI = 0.71 ± 0.06), *Bothus myriaster* (FI = 0.864 ± 0.502), *Gerres acinaces* (FI = 0.63 ± 0.06), *Fowleria aurita* (FI = 0.561 ± 0.497) and *L. fulviflamma* (FI = 0.67 ± 0.13).

The fulness index of the other species had a value between 1 and 3: *Fistularia commersonii* in the eastern creek (FI = 1.692 ± 0.218) and in the western creek (FI = 2.889 ± 0.802) and *Paramonacanthus barnardi* (FI = 1.066 ± 0.129).

Diversity of the diet

The diet was most diverse for *Lutjanus fulviflamma* (H'=0.89), *Paramonancanthus barnardi* (H'=0.81), *Apogon thermalis* (35-38 mm) (H'=0.79), *Fowleria aurita* (H'=0.77), *Apogon thermalis* (33-36 mm) (H'=0.74), *Mulloides flavolineatus* (H'=0.72) and *Gerres acinaces* (H'=0.71) (Fig. 5). This group corresponds to the species that mainly fed on benthic (hyper- and epibenthic) prey. A second group was characterised by a lower dietary diversity ranging from 0.4 to 0.55 : *Atherinomorus duodecimalis* (H'=0.44), *Lutjanus fulviflamma* (H'=0.45), *Stolephorus indicus* (70-75mm) (H'=0.51) and *Herklotsichthys quadrimaculatus* (H'=0.53). This group mainly fed on harpacticoids (except *Lutjanus fulviflamma*) and were considered to be 'planktivores' in this study. The diet of two species had an intermediate diversity : *Stolephorus indicus* (40-45mm) (H'=0.64) and *Bothus myriaster* (H'=0.66). The 'piscivores' *Plotosus lineatus* (H'=0.15), *Fistularia commersonii* (eastern creek) (H'=0.06), *F. commersonii* (western creek) (H'=0.18) and *Sphyraena barracuda* (H'=0.22) had the least diverse diet.

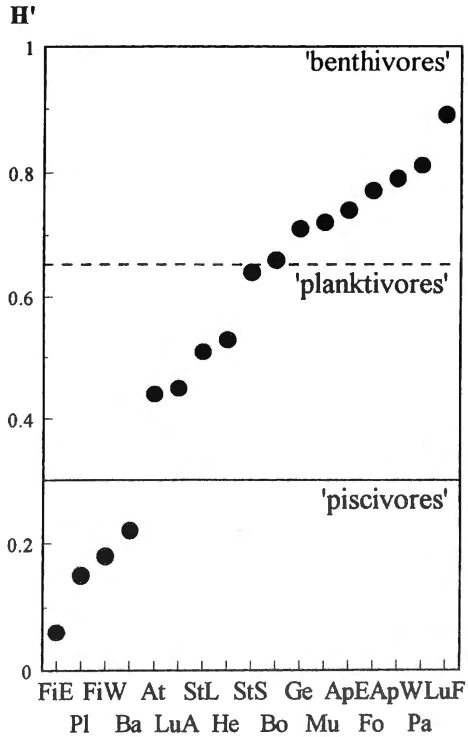

Fig. 5. – Diversity of the diet (Shannon-Wiener index H')

DISCUSSION

Based on the numerical and gravimetrical composition of the diet, the fulness index and the diversity of the diet four guilds (SIMBERLOFF & DAYAN, 1991) could be distinguished. *Herklotsichthys quadrimaculatus*, *Stolephorus indicus* and *Atherinomorus duodecimalis* were planktivores which mainly fed on harpacticoid and calanoid copepods and brachyuran zoeae and megalopae. They were characterised by a low fulness index and an average diversity of the diet of 0.53. These species mainly fed on planktonic prey. Harpacticoid copepods may also have been taken from the leaves of seagrasses, where they are very abundant (DE TROCH, unpublished data). The guild of the planktivores thus needs a broad interpretation. Species feeding on epiphytic organisms were also included in this guild. PARRISH (1989) separated the planktivores based on whether they feed on pelagic holoplankton or « demersal » meroplankton. VAN DER VELDE *et al.* (1994) used the guild planktivore/benthivore for species feeding on merozooplankton and benthic organisms.

The diet of *Apogon thermalis*, *Fowleria aurita*, *Paramonacanthus barnardi*, *Mulloides flavolineatus*, *Lutjanus argentimaculatus*, *L. fulviflamma* and *Gerres acinaces* was mainly composed of amphipods, tanaids and mysids. On average, their diet was very diverse (H'=0.74) and the fulness index was intermediate. They were considered to belong to the guild of the « benthivores ».

The data suggest that this guild can actually be divided in 3 subguilds, based on the sub-compartment of the benthos they preferentially utilise. Species feeding predominantly on mysids and amphipods (e.g. *Apogon thermalis*, *Fowleria aurita*) can be considered to be « hyperbenthivores » i.e. they feed in the water layers close to the substratum (the uppermost benthic compartment or hyperbenthal) where these taxa are known to occur abundantly (MEES & JONES, 1997 ; MEES, unpublished data). Species like *Paramonacanthus barnardi*, *Mulloides flavolineatus*, *Lutjanus argentimaculatus* and *L. fulviflamma* mainly consume tanaids, amphipods, isopods, molluscs, ostracodes, polychaetes... and can be considered to be « epibenthivores ». They feed on taxa that live in close association with the substratum or that are attached to the seagrasses. *Gerres acinaces* is an « endobenthivore », as shown by the high amounts of sediment in their stomach. They take their prey by filtering the sediment through the gills.

The food composition of *Plotosus lineatus*, *Fistularia commersonii*, *Sphyraena baracuda* and *Bothus myriaster* was dominated by fish and nektonic macrocrustaceans (caridean shrimp, large amphipods, crabs and mysids). Their diet had a very low diversity (average H'=0.15) and the fulness index was higher than that of the other species examined. PARRISH (1989) also used the guild of piscivores, while MORTON (1990) made a distinction between intermediate carnivores (feeding on macrobenthos and small fishes) and topcarnivores (exclusively feeding on fishes).

The trophic guild of « herbivores » (not encountered during the stomach analysis performed for this study) is broad and can also be divided into several subguilds. Species feeding on algae and seagrasses, as well as detritivores and corallivores were placed in this guild. Only juveniles of the corallivorous species were caught in the seagrass beds, where they are supposed to feed on non-corallivorous material. Some scientists have approached this problem by lumping herbivores and coral feeders together (PARRISH, 1989). « Non-carnivore » would be a better term instead of « herbivore ».

In the community of the western creek, half of the individuals (49%) were benthivores (Fig. 6A). This is correlated with the high densities of *Gerres acinaces* and *Lutjanus argentimaculatus*. Also planktivores were important in this community (40%). In terms of number of species (Fig. 6B), the community was also dominated by benthivores (37%). The high density of planktivores was attributable to a low number of species (7% of the total number of species in the community). This can be explained by the monospecific schooling behaviour of species like *Herklotsichthys quadrimaculatus*, *Stolephorus indicus* and *Atherinomorus duodecimalis*.

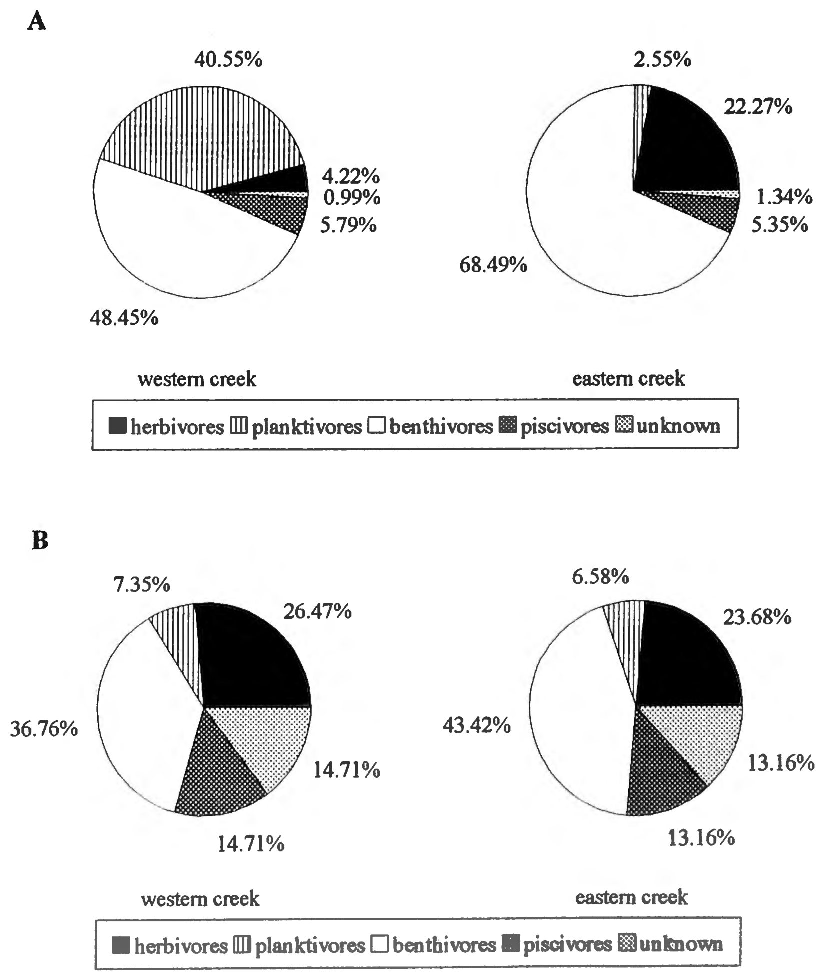

Fig. 6. – Trophic composition of the ichthyofauna occurring in the eastern and the western creek : (A) based on the densities, (B) based on the number of the species.

The fish community of the eastern creek was also dominated by benthivores (69% of the total density, Fig. 6A), corresponding to 43% of the total number of species (Fig. 6B). In this community, the densities and number of herbivorous species were remarkably higher (22% of the total density, 24% of the number of species) than in the community occurring in the western creek (less than 5% of the total density but 26% of the number of species).

It should be stated that the data obtained in this study were based on a single sampling campaign where mainly juvenile fishes were caught. The results and conclusions characterizing different guilds are thus based on dietary information for juvenile fishes. The same is true for the relevance of using niche breadth and fulness index. Additional data from a temporal study are currently being analyzed by E.O. Wakwabi.

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